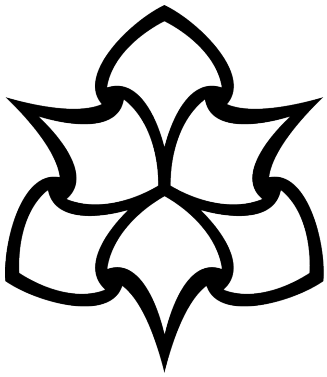

Vocal plasticity in a reptile

Henrik Brumm and Sue Anne Zollinger

Max Planck Institute for Ornithology, Communication and Social Behaviour Group, Eberhard-Gwinner-Straße, 82319 Seewiesen, Germany

Sophisticated vocal communication systems of birds and mammals, including human speech, are characterized by a high degree of plasticity in which signals are individually adjusted in response to changes in the environment. Here, we present, to our knowledge, the first evidence for vocal plasticity in a reptile. Like birds and mammals, tokay geckos (*Gekko gecko*) increased the duration of brief call notes in the presence of broadcast noise compared to quiet conditions, a behaviour that facilitates signal detection by receivers. By contrast, they did not adjust the amplitudes of their call syllables in noise (the Lombard effect), which is in line with the hypothesis that the Lombard effect has evolved independently in birds and mammals. However, the geckos used a different strategy to increase signal-to-noise ratios: instead of increasing the amplitude of a given call type when exposed to noise, the subjects produced more high-amplitude syllable types from their repertoire. Our findings demonstrate that reptile vocalizations are much more flexible than previously thought, including elaborate vocal plasticity that is also important for the complex signalling systems of birds and mammals. We suggest that signal detection constraints are one of the major forces driving the evolution of animal communication systems across different taxa.

1. Introduction

Signal plasticity, i.e. the capacity for individual phenotypic signal adjustments in response to changes in the environment, is considered a crucial step in the evolution of animal communication systems [1,2]. Thus, elucidating the phylogenetic origins of this faculty is important for understanding the diversification and versatility of signals in general [3–5]. In acoustic communication, an important form of signal plasticity is related to communication in changing social or physical environments, and many studies have shown special capacities of birds and mammals in these contexts (e.g. [6–10]). One particular mechanism of such vocal plasticity is the Lombard effect, in which a signaller adjusts the amplitude of a vocalization depending on the level of masking noise, which allows maintaining communication when signal transmission is impaired [11]. The Lombard effect is well studied in human speech and has also been found in other mammals and birds [12,13]. As in human speech, the Lombard effect in birds, bats and monkeys is often, but not always, accompanied by an increase of the duration of brief sounds [12], which further increases the detectability of the signals in noise [14–16].

Despite the previous research into the mechanisms of vocal plasticity, the evolution of the Lombard effect and other forms of vocal plasticity are largely unknown because previous studies investigated mainly birds and mammals. A recent study suggests noise-dependent regulation of call amplitude in a frog [17], whereas another study found no evidence for the Lombard effect in another anuran species [18]. In addition to the unresolved situation in anurans, the non-avian reptiles have been entirely neglected (although birds are members of Dinosauria, and therefore Reptilia, to avoid confusion, we will continue to (incorrectly) use the term reptile to refer to all members of this group except birds) leaving a critical gap in our understanding of the evolution of vocal plasticity. Although many reptiles use sound to communicate (reviewed in [19]) it remains unclear whether they possess any form of vocal flexibility to adjust their vocal

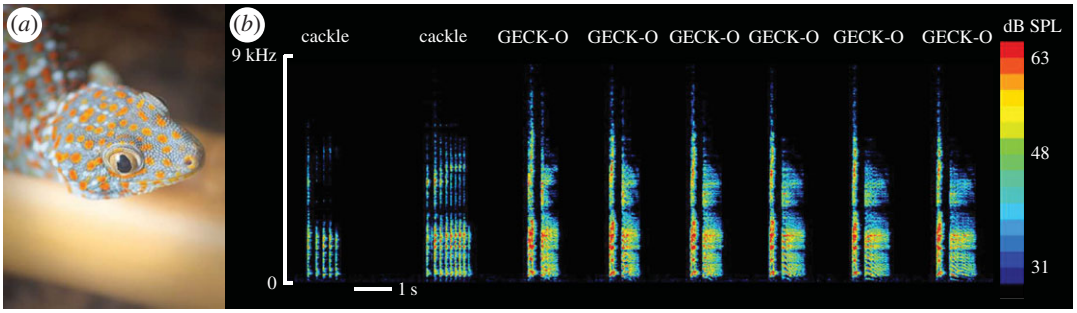

Figure 1. Advertisement call of the tokay gecko. (*a*) A male tokay gecko (photo by Frank Lehmann). Males of this species produce loud advertisement calls that are used for territory defence and mate attraction. The names 'tokay' and 'gecko' are derived from the second part of the advertisement call of this species. (*b*) Spectrogram of a typical advertisement call series consisting of two soft cackles followed by high-amplitude GECK-O syllables. In our sample of six males, the GECK notes were on average 7 dB higher in amplitude than the cackles. (Online version in colour.)

signals to the environment. To trace back the evolutionary origin of the complex vocal plasticity found in birds and mammals, we investigated whether a lizard, the tokay gecko *Gekko gecko* (figure 1*a*), modifies the properties of its calls in response to changes in background noise. Tokay geckos have a range of different vocalizations for communication, including a loud advertisement call that is used by males to attract females and to repel rival males [20]. These advertisement calls typically consist of two different call types: low-amplitude cackles followed by much louder GECK-O syllables (figure 1*b*). If tokay geckos exhibit the Lombard effect, then they will regulate the amplitude of a given vocalization type (i.e. cackles, GECK notes and O notes) depending on the level of background noise. Since the Lombard effect can be accompanied by additional signal changes [12], we also investigated whether the geckos adjust the duration of their call types or the number of syllables per call series in noise.

2. Material and methods

(a) Subjects and advertisement call

Tokay geckos are nocturnal lizards from South-East Asia, well known for their conspicuous advertisement calls [21]. The words 'gecko' and 'tokay' are both onomatopoeia of the loud part of the advertisement call of this species. This call typically consists of one or several soft cackles followed by several loud GECK-O syllables (figure 1*b* and electronic supplementary material). The cackles are also referred to as 'rattles', and the GECK-O syllables as 'binotes' or 'tok-kay syllables' [20,22]. We recorded the advertisement calls of captive-bred male tokay geckos under different noise regimes. All geckos were kept in individual terraria, maintained at 25–30°C, 60–80% air humidity and with a 12 : 12 hours light cycle. The animals had ad libitum access to water and were fed twice a week with live insects that were regularly dusted with minerals, vitamins and trace elements.

(b) Experimental set-up

Gecko calls were digitally recorded with a sample rate of 44.1 kHz and 16 bit accuracy using an omnidirectional Sennheiser ME 62 microphone, whose signal was fed through a SM Pro Audio PR8E preamplifier into to an external Roland UA-25EX soundcard that was connected to a computer running the acoustic recording and analysis software Sound Analysis Pro 2011 [23]. Two loudspeakers (JBL Control 1 Pro) broadcast white noise that was played from a computer through a Technics SU-V300M2 amplifier. The noise had a frequency range from 0 to 12 kHz (electronic supplementary material, figure S1), which covers the entire hearing range of the species [24,25].

In total, we tested seven male tokay geckos. Six of them were kept individually in a terrarium (50 × 50 cm and 70 cm high, with a plastic mesh top and sides) in a room lined with acoustic absorbers (Basotect Pyramid 70 mm) and one male was recorded in a different set-up (see below). The vocalizations of each of the six males were continuously recorded for a period of 4 days. The microphone was placed facing downwards 1.2 m above the centre of the terrarium top. The two loudspeakers were mounted at opposing sides 0.3 m from the terrarium facing towards the centre of the container. The volume of the amplifier was set so that the noise amplitude ranged between 60–65 dB(A) (re. 20 µPa, all following dB values refer to same standard reference), as measured with a Casella CEL-240 SPL metre inside the terrarium. During the recording session, 24 h periods of broadcast noise were alternated with 24 h periods of silence. Ambient noise levels in the recording room ranged between 32 and 35 dB(A). Three males received the noise treatment first; the other three received the control treatment first. All but one male called in both treatments and this one individual was excluded from the analysis. From the five remaining males, we recorded, on average, 14 cackle calls and 37 GECK-O syllables (electronic supplementary material, table S1).

One additional male was recorded continuously for 37 days in a larger terrarium (95 × 50 cm and 120 cm high), in which it was housed individually. In this set-up, the microphone was placed 1 m in front of the 95 cm-wide terrarium front, pointing at a point 20 cm below the upper edge and halfway between the sides (i.e. the centre of the top third of the terrarium). The loudspeakers were placed facing downwards on top of the terrarium. In this long-term recording session, noise was broadcast for 1 or 2 days interspersed with silent periods of the same durations. Since this terrarium was considerably larger than the test terraria used for the other subjects, the position of the animal in relation to the microphone could vary to a higher degree. To reduce the variability of the recorded call amplitudes owing to the position of the animal, we only included calls that were emitted in the top third of the terrarium. To this end, the gecko was monitored with a video camera (Panasonic SDR-S50). To ensure that the animal was visible on the video recordings also during the night (when most calls are produced), the terrarium was illuminated at night with low-intensity blue LED light. In the top third of the terrarium, the noise level ranged between 60 and 64 dB(A); ambient noise when the playback was off was 30–38 dB(A). Altogether we analysed amplitudes and temporal parameters from 92 call series with a total of 220 cackles and 519 GECK-O syllables from this male (electronic supplementary material, table S1). After the experiment (i.e. under ambient noise conditions), we also noted the number and type of call types for an additional 162 call series from this individual.

(c) Acoustic analyses

For each call series we counted the number of different call types and measured their amplitude. All acoustic measurements were done with the analysis software Avisoft SASLab Pro v. 5.2 (Avisoft Bioacoustics, Berlin, Germany). Peak rms amplitudes were measured with an integration time of 10 ms. The background noise amplitude was subtracted from the measured amplitude values following published procedures [12]. We also measured the duration of GECK notes and O notes. This was done in waveforms at an amplitude threshold of −10 dB below the peak amplitude [26]. Prior to the measurements, we high-pass filtered all digital files to increase the overall signal-to-noise ratio by removing some of the noise below the frequency band of the gecko calls (finite impulse response filter, cut-off frequency 100 Hz, Hamming window 1024 taps). The temporal resolution of the measurements was 1.5 ms. We did not measure the duration of the cackle syllables because some of the softest cackle pulses had a signal-to-noise ratio of less than 0 dB in the noise condition and therefore reliable duration measurements were not possible. We did not measure spectral call parameters because they were affected by the noise treatment.

(d) Statistical analyses

The effect of the treatment (noise/no noise) on amplitude, duration, and the number of call types was examined with separate models in R (v. 3.0.2; http://www.R-project.org/) using the package lme4 [27]. In each model the individual and the call series were fitted as random effects to control for the repeated measures design. The treatment effects on amplitude and duration were investigated with linear mixed models (LMMs), model residuals were checked visually. The effect on the number of call types was examined with generalized linear mixed models (GLMMs), in which the count data were fitted with a Poisson distribution and a log link function. In a next step, we analysed whether the noise treatment affected the duration of the first GECK and the first O note of each call series by fitting LMMs with individual as random effect to account for the repeated measures design. We assessed the effect of noise exposure on call parameters by comparing models including treatment to null models using likelihood ratio tests with one degree of freedom.

The relationship between the number of cackle calls and the number of GECK-O syllables in a call series was investigated with Spearman rank correlations (using SPSS Statistics 21). This was done with two data sets: (i) across all males that produced at least five call series, from each of these ($n = 5$ males) we randomly selected five call series independent of the treatment, and (ii) within the one male from which we recorded the highest number of calls ($n = 254$ calls).

3. Results

Our analysis of GECK and O notes reveals that the lizards increased the duration of their call syllables in noise (figure 2*a*,*b*). GECK notes produced in noise were 7% longer on average than those uttered in the control condition ($\chi^2_1 = 4.367$, $p < 0.05$), and O notes were 37% longer ($\chi^2_1 = 50.059$, $p < 0.001$). This effect can be accounted for partly by the fact that the geckos produced longer series of GECK-O syllables in noise (see below) and that the duration of GECK and O notes tended to increase along with increasing numbers of syllables in a series. In addition, we also found evidence for a noise-dependent regulation of individual call durations—when considering only the first syllable of each GECK-O series, GECK notes were 5% longer, on average, in noise compared to the silent control condition ($\chi^2_1 = 5.759$, $p < 0.05$), and O notes were 19% longer ($\chi^2_1 = 24.799$, $p < 0.001$).

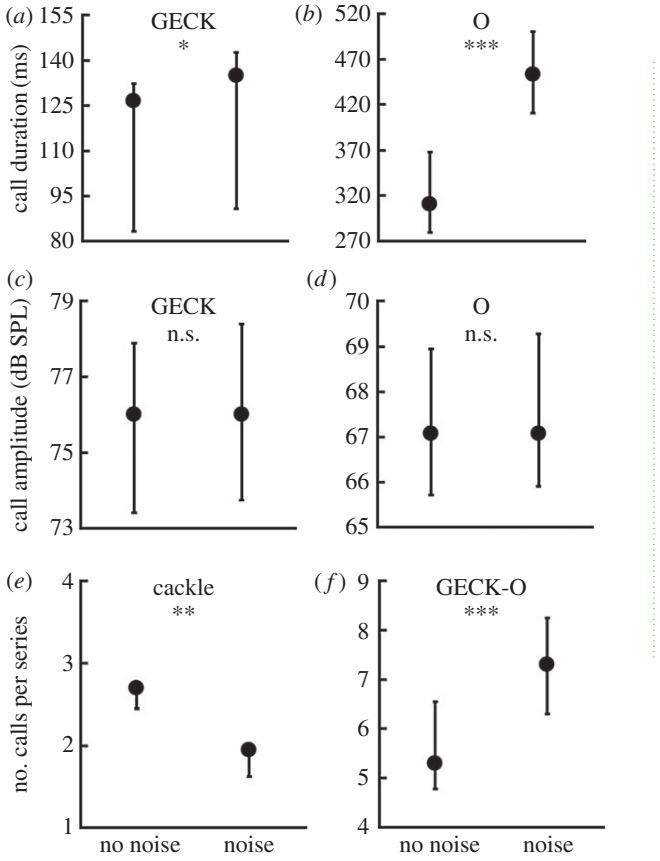

Figure 2. Changes in tokay call parameters in relation to background noise. Grand averages (medians and interquartile ranges) of (*a*) GECK-note duration, (*b*) O-note duration, (*c*) GECK-note amplitude, (*d*) O-note amplitude, (*e*) number of cackles per call series, and (*f*) number of GECK-O syllables per call series. The noise was played back at sound pressure levels between 60 and 65 dB(A) (re. 20 µPa) at the position of the animal. $n = 6$ males.

Within individuals, mean call amplitudes differed less than 1.3 dB between the two noise conditions and we found no statistically significant differences between the two treatments (GECK: $\chi^2_1 = 2.361$, $p = 0.124$; O: $\chi^2_1 = 3.4668$, $p = 0.063$; figure 2*c*,*d*; and cackle: $\chi^2_1 = 3.296$, $p = 0.069$). The low *p*-values of the amplitude difference in O notes and cackles are not hinting at a potential Lombard effect because the mean model estimates were lower in noise compared to the no-noise condition (electronic supplementary material, table S2), which is the opposite of what is predicted by the Lombard effect. Further, the predicted sizes of these amplitude differences were negligibly small (0.5 and 0.7 dB). Thus, we found no evidence for the Lombard effect in the tested geckos.

However, the lizards used a different strategy to increase the overall amplitude of their call series: instead of increasing the amplitude of the call notes, they produced more of the loud GECK-O syllables and fewer of the softer cackle calls in noise (cackles: $\chi^2_1 = 10.568$, $p < 0.01$; GECK-Os: $\chi^2_1 = 17.117$, $p < 0.001$; figure 2*e*,*f*). Hence the geckos traded the number of low-amplitude and high-amplitude syllables in each call series to produce more of the louder notes in noise. This regulation of syllable numbers in noise reflected a general, negative correlation between the numbers of the two syllable categories: independent of the background noise, an increase in the number of cackles resulted in a

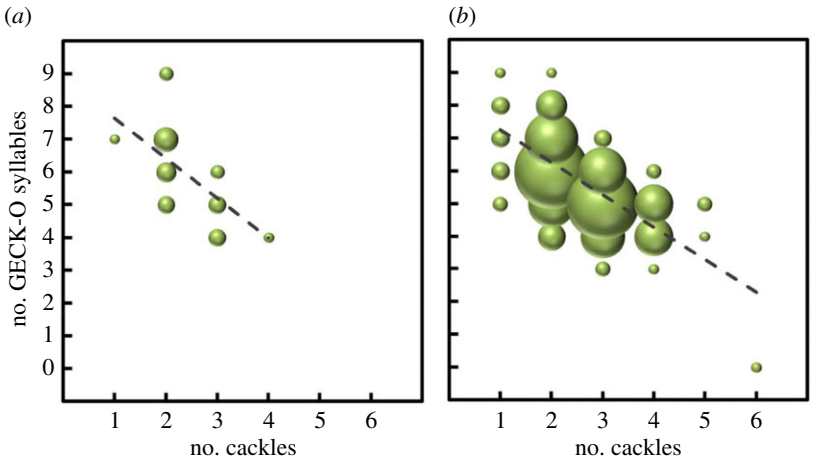

Figure 3. Correlation between the two syllable types within tokay call series. (*a*) A sample across five males with five randomly selected calls from each ($n = 25$ calls). (*b*) All calls from the male from which we recorded the highest number of calls ($n = 254$ calls). The size of the bubbles represents the number of observations, ranging from 1 to 6 in (*a*) and from 1 to 52 in (*b*). (Online version in colour.)

reduction of GECK-O syllables (across individuals: $\rho = -0.743$, $n = 25$, $p < 0.01$; figure 3*a*; within the individual with the most calls: $\rho = -0.605$, $n = 254$, $p < 0.01$; figure 3*b*).

4. Discussion

The results of our study establish for the first time, to our knowledge, that a non-avian reptile adjusts its calls in relation to environmental noise. We found that the tested geckos increased the duration of their call syllables in response to experimental noise, demonstrating that a regulation of signal duration is not restricted to birds and mammals. The magnitude of the increase in O-note duration in noise was similar to the effects that have been reported for monkey calls and human speech [28–30]. In birds and mammals, increases in the duration of brief acoustic signals in noise are thought to be adaptations to the temporal summation of signal energy in the auditory system of receivers [16,29,31], which makes longer sounds easier to detect in noise [14,15]. To our knowledge, no studies on temporal integration in reptile hearing are available to date. However, comparative neurophysiological data suggest that integration functions are similar across vertebrates including goldfish (*Carassius auratus*) [14] and thus we may assume that auditory thresholds of reptiles are also reduced by an increase in the duration of brief sounds. Consequently, by producing longer calls in noise the geckos would maintain signal transmission because longer calls would be easier to detect in noise. Such a link between signal production and perception provides a striking example of sender-receiver coevolution in a reptile communication system, similar to what is found in birds and mammals.

Unlike birds and mammals, the tested geckos did not exhibit the Lombard effect, i.e. they did not increase the amplitude of their call syllables in relation to the background noise level. However, instead of increasing the amplitude of each call component, they produced more of the loud GECK-O syllables and fewer of the softer cackle calls in noise. Thus, despite the lack of the Lombard effect, the animals were able to increase the overall signal-to-noise ratio of their calls, and, as a consequence, reduce the auditory masking of their vocal signals. This plasticity in syllable type selection in geckos can be regarded as an alternative strategy to the Lombard effect and it is similar to what has also been found in avian sauropsids: urban birds that are exposed to high levels of anthropogenic noise chose preferentially those song notes from their repertoire that can be produced at particularly high amplitudes [32]. However, unlike the lizards tested in this study, birds also use the Lombard effect to further enhance the intensity of their vocalizations in noise [12]. Perhaps tokay geckos are unable to increase the amplitude of their mating calls because they are calling close to their physical limitations, as is thought to be the case in some frogs (reviewed in [33] but see [17]).

The absence of the Lombard effect in a lizard is consistent with the hypothesis that noise-dependent regulation of vocal amplitude has evolved independently in birds and mammals [12,34]. Since the Lombard effect is very robust, i.e. in species that exhibit the trait, it is typically detected in every tested individual (e.g. [29,35–37]), we are confident that the lack of the effect in a small number of tokay geckos is informative. Like Cope's grey treefrogs, *Hyla chrysoscelis*, [18], the geckos did not increase the amplitude of a given call syllable in response to an increase in the background noise. Thus the Lombard effect in tungara frogs, *Engystomops pustulosus*, [17] is likely to be a convergent trait that has evolved in parallel to the independent occurrences of the Lombard effect in birds and mammals. Most anurans produce vocalizations with the vocal folds in their larynx [38] and some species can adjust the frequency parameters of their calls in response to changes in the social environment [39]. Perhaps differences in motor control over subglottal air pressure during phonation may account for the occurrence of the Lombard effect within the anuran clade.

Vocal signalling is a less common feature in reptiles than in anurans, with many taxa producing only non-vocal sounds, such as percussive sounds or hissing, generated by forceful expiration of air without involving the vocal cords. Among the vocal reptiles (some chelonians, some lizards - most notably geckos, and crocodilians (reviewed in [19,40])), the functional morphology of their vocal systems are quite diverse, as are the complexity of signals produced, which range from noisy grunts that require little control of glottal tension to frequency-modulated tonal sounds requiring active control of the vocal cords [19]. Basal sound production mechanisms, such as hissing or grunting are more inflexible in their production than tonal, harmonic

and frequency modulated sounds, which are modified by changes in tension of the vibratory tissues, and thus the evolution of more sophisticated vocal anatomy may be a first step towards the evolution of flexible acoustic communication systems, such as those of birds, mammals, and now geckos.

In addition to the plastic syllable-type selection we also discovered a negative correlation between the numbers of the two syllable categories of a call, independent of the background noise: an increase in the number of cackles resulted in a reduction of GECK-O syllables and vice versa. This finding suggests a physical constraint during sound production that limits the overall number of calls in each call series. Such a limitation could come about by muscle fatigue or the respiratory pattern underlying phonation, for instance when a call series is produced during one expiration (i.e. no inspirations between successive syllables of a series) and the animal eventually runs out of air to produce more syllables. A respiratory vocalization constraint in lizards seems plausible because, unlike birds or mammals, they do not have a diaphragm [41] or air sacs [42] that increase the efficiency of breathing. In terms of motor planning by the brain, our results suggests that the serial organization of a call series is already established at the switch between call types, as only a decision about the number of cackle calls is required to determine the entire sequence.

It remains to be shown whether the observed noise-induced changes in the number of call types affect the information content of the whole call series. Like tokay geckos, male túngara frogs may vary the number of two calls types in their mating signals [43], and it has been shown that this signal compositionality carries contextual information that is relevant in terms of intra- and intersexual selection [44]. However, it is not known whether cackles and GECK-O calls differ in their function, and thus it remains unclear whether the vocal adjustments of the geckos to maintain communication in noise may compromise the information encoded in the signal sequence.

The surprising vocal plasticity in geckos reported here parallels findings from visual communication in other lizard species that increase the intensity of their visual displays to maintain communication when the optic background impairs signal detection [45,46]. This convergent evolution suggests general principles of communication independent of the signal modality, with signal detection constraints being one of the major forces driving the evolution of animal communication systems [47,48].

Our findings demonstrate that vocal signalling in reptiles may be much more flexible than previously thought, including vocal traits that are crucial for the more sophisticated communication systems of birds and mammals. The results of our experiment therefore challenge the common view that the evolution of flexible acoustic communication is restricted to birds and mammals.

Ethics. All procedures described in this manuscript were conducted in accordance with appropriate German regulations and the guidelines for the treatment of animals in behavioural research and teaching of the Association for the Study of Animal Behaviour (ASAB).

Data accessibility. The data used in our analysis can be found in the electronic supplementary material.

Authors' contributions. H.B. designed the study and carried out the experiments. H.B. and S.A.Z. analysed the data and wrote the manuscript.

Competing interests. We have no competing interests.

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